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A SKETCH OF COMPARATIVE EMBRYOLOGY.

I.—THE HISTORY OF THE GENOBLASTS, AND THE THEORY OF SEX.

BY CHARLES SEDGWICK MINOT.

THE series of articles, of which this is the first, is intended to present in a simple and popular manner, the leading results of the very numerous researches upon the development of animals, published during the last fifteen years. These researches have completely altered the whole science of comparative anatomy and animal morphology, by entirely upsetting a large part of Cuvier's classification and the idea of types upon which it was based, substituting the demonstration of the fundamental identity of plan and structure throughout the animal kingdom from the sponges to man. The details of the observations are already too many for any but the most industrious specialist to become familiar with. We have now entered upon the period of generalizations, which are already so numerous and important that it is impossible to study scientific zoölogy without some knowledge of them. This great progress is still so recent that its results have not been transferred to the text-books, nor even gathered together in any scientific review. Nevertheless, it is possible to compile an outline which may be accepted as fairly correct. This outline it is my present object to trace, with the hope that it may prove at once accurate and useful.

Each branch of the subject will be treated by itself. The illustrations will be taken mainly, if not exclusively, from pen drawings prepared by myself for a work on Comparative Histology, upon which I am engaged. The original source of each figure will be given.

The arrangement of topics will be, first the structure of the egg and spermatozoön; second, the phenomena of impregnation; third, segmentation and the formation of the germ-layers; fourth, the essential features of the embryology of the leading animal types, beginning with the simplest and ascending to the most complicated and highest.

The starting point of comparative embryology, as indeed of nearly all branches of biology, is the cell, composed of the nucleus surrounded by protoplasm. A few years ago the theory was advanced that the nucleus was unnecessary, and various observations were adduced to show that in a considerable number of

living objects there was nothing but protoplasm. In accordance with this view this substance was called the "Physical Basis of Life," under which name it has been much paraded before the public. By a great many persons protoplasm is conceived and described as a "simple mass of jelly." By an easy illogic this phrase of the very ignorant becomes a demonstration that life is a mere property of matter—but that is no matter to us now. What does concern us, is that protoplasm is not a mere simple mass of jelly, but is certainly very complicated, perhaps so complicated that its constitution is beyond the power of human conception. One of the visible indications of the complexity of protoplasm, is, that it is not a continuous substance, but interrupted by vacuoles or cavities, which vary in size, shape and number. These cavities are usually round or oval. The protoplasmatic partitions between them form a complicated network. Sometimes the cavities may fuse together, by a breaking through of the partitions, in which case the network is reduced to a number of connecting threads. The cavities are not empty, but filled with various substances, sometimes liquid, sometimes solid, and differing in chemical composition, as the protoplasm is from one kind of cell or another. For the contents of the vacuoles I propose the name *enclosures*. It will be seen that protoplasm forms only the network which surrounds the other substances. This is an important fact, without knowing which, it is impossible to understand the formation of eggs.

Let us return to the nucleus. It has been asserted that there are numerous animals (*Monera*, etc.) mostly microscopic, which consist solely of protoplasm without any nucleus, and also in some cases that the egg-cell ejects its nucleus, and then it is called a *cytode*. Now it has been shown that a very large proportion of these un-nucleated protoplasms (*Protista*) really have a nucleus, and are unicellular animals or plants; therefore it is *probable* that no protoplasm can live without a nucleus, that is to say without being part of a cell.¹ So also with the egg; it has become probable that it never loses its nucleus.

The result of these discoveries is to reëstablish the full importance of the *cell*, as the unit of animal and vegetable organization. Recent investigations by Bütschli (No. 18) and Engelmann upon

¹ The reader must remember, however, that a number of minute organisms exist in which no nucleus has been observed. Future research will decide whether the absence of the nucleus is real or apparent.

the Infusoria have strengthened the movement of return towards the earlier doctrine, which had been for a while crowded aside by the over-hasty advocacy of the protoplasm theory. Bütschli especially has made it extremely probable that all Infusoria are but highly specialized and curiously modified unicellular beings.

It is certainly safe to assume for the present that no life can exist outside of cells, and that all the phenomena of development must be reduced to terms of cell-life. The first point, therefore, to be settled is the relation of the sexual products to the cells from which they are derived, and the multiplication of which they effect. I shall give an hypothesis of these relations, which I have formed, and which is the only one, so far as I am aware, yet proposed. Whether this hypothesis will ultimately prove correct or not, it is impossible to foresee. As it still appears to me plausible, I shall venture to reproduce it here. To explain it, it is necessary to premise brief accounts of the structure of the sexual products (genoblasts) and their development. We will begin with the egg.

The essential part of every egg is developed from a single cell, which undergoes certain modifications, probably nearly the same in all animals, thereby acquiring the definite characteristics which distinguish it as an *egg-cell* from an ordinary cell, and from all other specialized forms of cells.

The eggs of different classes and even species of animals are, as is well known, extremely unlike in appearance. The dissimilarity refers chiefly to size, and to the nature and number of membranes or envelopes by which the egg-cell proper is surrounded by the parent. Thus in the hen's egg, the yolk alone represents the part formed by the egg cell, while the white of the egg and the egg-shell are only secondary envelopes, the former serving to nourish, the latter to protect the yolk, which is the essential part, the true egg.

Now, it is well known that mere size does not enter into the determination of the real affinities of animals and plants. The smallness of the rat does not show that it is related to the frog rather than to the elephant, and from our present point of view the size of eggs is meaningless. The egg-cells are large in all birds and reptiles, in the sharks, rays, ganoids and Cephalopoda, small in mammals, bony fishes and nearly all invertebrates, intermediate in amphibians.

The various envelopes which eggs ever have, may be classed under four categories: *First*, a very thin and delicate one, the proper membrane of the cell itself, which ought always to be distinguished as the vitelline membrane; *second*, the ovarian envelope which is secreted around the egg-cell by the tissues of the ovary; *third*, the envelopes secreted by the oviduct, which may form an envelope of nutritive matter, or a protective shell, or both, as in the hen's egg, of which the nutritive white is secreted by the upper part, the calcareous shell by the middle part of the oviduct; *fourth*, coverings secreted by accessory glands, such as the slime in which the eggs of snails are imbedded, or the shells in which leeches lay their eggs. By adhering to this classification the student will be able to follow with profit the labyrinth of special description. To enter into further details would lead aside from the object of this article: let it suffice to have pointed out the possibility of manifold variations, and to have emphasized the fact that the egg-cell is the important and only essential part of an egg.

The egg-cell always arises from a germ-mass, called *Keimlager* in German. The germ-mass is at first composed of cells all essentially identical in microscopic appearance. Single isolated cells then transform themselves into eggs, while their surrounding fellow-cells play the rôles of nurses and purveyors. To avoid inaccuracy it must be added that in some cases the germ-mass does not consist of distinct cells, but contains numerous nuclei which ultimately become the centers of distinct cells; but before this separation the differentiation of the ova begins. In both methods of development some cells enlarge to form the eggs, others supply the enlarging and growing cells with nutritive material. It is impossible to enter upon this subject further than to say that the form and disposition of nutritive cells varies extremely in different animals, while the changes in the egg are much more uniform, so that it is possible to describe in general terms the development of the ovum.

The modifications which occur in the growing egg-cells are as follows:

1. Change of size: the cell enlarges, it being a rule, no exception to which is, I believe, known, that the mature egg-cell is much larger than any of the other cells in the body of the parent.
2. Change of shape: the cell becomes nearly or quite spherical.

3. The nucleus becomes larger, spherical, and assumes an eccentric position within the cell, while the meshes of the nuclear network are coarse, and few, and for the most part radiate from the nucleolus, which is large, distinct, highly refringent and placed eccentrically within the nucleus.
4. The cellular network becomes very distinct, its interspaces are filled with ovoid or round, solid enclosures, which are usually if not always mainly of an albuminoid character. These enclosures form the part which is called the deutoplasm by Edouard von Beneden and others. The deutoplasm causes the egg-cells to be called the yolk, because it is the nutritive matter from which the protoplasm of the cell grows. The term yolk has no very exact scientific meaning, for it is used to designate sometimes the deutoplasm alone, sometimes the whole egg, as when the segmentation of the yolk is spoken of.
5. A cell membrane appears, and usually acquires considerable thickness,

A typical mature egg-cell is shown in Fig. 1, which represent the ripe ovum of *Toxopneustes lividus*, the common sea-urchin of Europe. The nucleus is proportionately larger than in the eggs of many other animals, its contents are fluid except the net-work and the nucleolus (*n*), which latter frequently has one or more

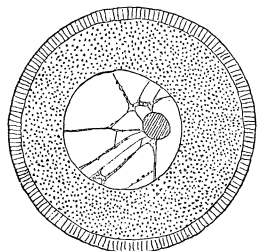


FIG. 1.—Mature ovum of sea-urchin, after O. Hertwig.

vacuoles. In some cases there are several or many nucleoli, as in osseous fishes, but the meaning of this difference is absolutely unknown. Moreover, this egg is unlike that of many animals in that the yolk spherules or the deutoplasm granules are comparatively small, while in some animals, especially those with larger eggs, the granules are larger. If these variations are borne in mind the figure given may be accepted as a correct representation of a mature egg-cell.

I am inclined to think that besides these peculiarities the ripe egg-cell shows a distinction between a thin denser peripheral layer of protoplasm immediately under the vitelline membrane and a central portion, which alone contains deutoplasm, recalling the differentiation of the ectosarc and endosarc in the *Amœba*. This feature has been observed in several cases, and further research may demonstrate it to be common to all eggs.

The shape of the egg does not necessarily remain spherical, but may be altered by external pressure, as when several are laid in one capsule (*Lumbricus*, *Nephelis*, *Planaria*, etc.), or when compressed by an unyielding shell. A very striking instance has recently been described by Repiachoff in the Supplement to Vol. xxx of the *Zeitschrift für wissenschaftliche Zoologie*. He describes the egg of *Tendra zostericola* (a European Bryozoön found on eel-grass) as having a fusiform shape, Fig. 2.

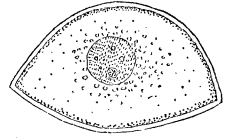
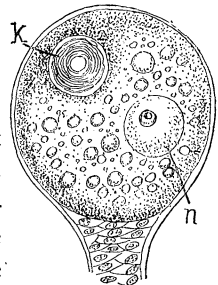


FIG. 2.—Egg of *Tendra zostericola*, after Repiachoff.

One other remarkable modification of the egg-cell occurs among spiders, and has not yet been observed in other animals. The eggs of some spiders (Fig. 3) contain, besides the nucleus, a second body, *k*, of about the same size as the nucleus, solid and resistant, and exhibiting indications of a series of concentric laminæ; this is probably only a specialized form of deutoplasm, similar to the four large oil globules described by Spengel in the eggs of *Bonellia viridis*.



When an egg-cell attains maturity, the first important and striking change that occurs is the translation of the nucleus close to the surface of the egg, where it disappears. The nucleus of the ripe ovum is usually called the germinative vesicle, and the phenomenon just alluded to is still generally termed the disappearance of the germinal vesicle. The fact has long been known, but was entirely inexplicable

FIG. 3.—Egg-cell of *Tegenaria domestica*, after Balbiani; *n*, nucleus; *k*, laminar body.

until the discoveries of the last few years afforded a partial explanation, by rendering it probable that the disappearance is not real but only apparent. The subject is still obscure, because the observers are not entirely agreed with one another as to the facts. The greatest difficulty arises from the fact that in most cases the egg-cell ejects two or three small bodies over the spot where the nucleus disappears. These bodies are called polar globules, and are known to occur in Coelenterates, Echinoderms, Molluscs, various classes of worms, Tunicates, Ganoids and mammals, so that their existence in all cases might fairly be assumed, were it not that renewed special search for these bodies in Amphibia, by O. Hertwig, had failed to discover any trace of them. No

satisfactory observations of the polar globules of the eggs of any of the Rotifera or Arthropoda have yet been made; but, as the interest in this subject is very recent, the globules may yet be found in those classes.

When the polar globules *are* formed, the following events may be *assumed* probably to occur. Ed. van Beneden's account of the development of the polar globules in the rabbit may be especially mentioned as exceptional. The history as here given is based upon observations made upon a limited number of invertebrates. When the nucleus disappears it is replaced by a spindle-shaped body known as the *kern-spindel* or Anglice *nuclear spindle*, which is generally regarded as the metamorphosed nucleus. It consists (Fig. 4) of a small number of fine, parallel threads, which, converging towards either end, run out into two points. The fibres are all thickened in the middle at the same level; these thickenings produce the appearance of a distinct plate or disk in the middle (Strassburger's *Kernplatte*). It will be convenient to adhere to the term nuclear plate to designate these thickenings. The spindle lies perpendicular to the surface of the egg. The pointed end of each spindle occupies the center of a clear space, from around which radiate fine threads, thus producing a sun-like figure. The whole spindle, with the two suns, has been named the *amphiaster*.

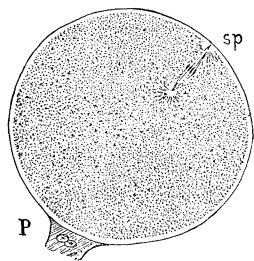


FIG. 4.—Ovarian egg of *Hæmopsis*, after Hertwig; *sp*, nuclear spindle; *p*, peduncle attaching the egg to the ovary.

The character of the next series of changes is shown in Fig. 5. The spindle is partly excluded from the egg, one end projecting outwards and enclosed by a distinct mass of protoplasm, constricted around the base. The “*kernplatte*” has divided in two, one-half moved towards either end of the spindle. The spindle next divides and the inner moiety retreats into the egg, the outer into the protuberance, which thus becomes the first polar globule. The part of the spindle within the egg, transforms itself into a second spindle, which develops a second globule like the first. Frequently a third globule is also formed. The connection of the globules with the yolk lasts some time, and in the case of leeches is not dissolved until segmentation begins. These globules take no part in the further history of the egg; they disappear—how, is not

exactly known. The part of the spindle in the egg-cell, returns to the center of the egg and becomes a nucleus-like body, now termed the *female pronucleus*.

The egg-cell, therefore, divides into two parts, first, the egg proper with the female pronucleus, second, the polar globules. The egg-cell has become not as a whole, but partly, a real egg, the ultimate female sexual product. Since the use of the term egg cannot be restricted, and since precision of nomenclature is, in this case, particularly desirable, I have proposed the name *thelyblast* for the female element.

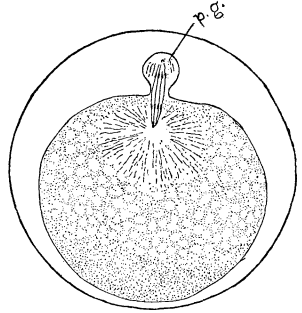


FIG. 5.—Egg of *Nephelis* three-quarters of an hour after laying. Formation of the first polar globule, after Hertwig.

We pass now to the history of the male elements, or spermatozoa, concerning which the observations of naturalists have been even less satisfactory. The adult spermatozoa have, with a few exceptions, an elongated, almost thread-like form, Fig. 6, and consist of a shorter and thicker portion, the head, *a*, a short middle piece, *b*, and a filiform tail, *d*, from which is suspended, in many vertebrates, a thin and very transparent undulating membrane, *c*. Innumerable modifications of this type occur by variations in the size and shape of the head and the length and thickness of the tail. In a few exceptional cases, as among the nematode worms, the spermatozoa exhibit absolutely no trace of this form, but are apparently constructed upon an entirely distinct type. A few species of invertebrates have two forms of spermatozoa.

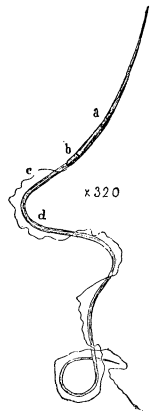
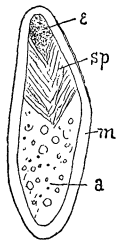


FIG. 6.—Fresh spermatozoon of *Salamandra maculosa*, after Gibbes. *a*, head; *b*, middle piece; *c*, membrane; *d*, tail.

In a not inconsiderable number of invertebrates, we find so-called spermatophores. These are only bundles of spermatozoa enclosed in a protective covering or shell (Fig. 7). In *Cyclops* this shell is secreted by the efferent duct, around the spermatozoa, just as the shell is secreted around the eggs by the oviduct. The spermatophores of some animals exhibit a very complicated structure, and have curious forms.



46.

FIG. 7.—Spermatophore of *Cyclops quadricornis*. *m*, covering membrane or shell; *sp*, spermatozoa.

Like the eggs, or thelyblasts, the spermatozoa are developed out of cells, each cell forming not one sexual element, as in the case of the egg, but several. Hence several young elements appear within the interior of one cell at once; therefore this one cell is called the *spermatocyst*,¹ while the young elements which are to become spermatozoa, are called *spermatoblasts*, and lie within the mother-cell or the cyst. The spermatoblasts appear at first as cell-like, spherical bodies, which may multiply by division within the mother-cell. Their development progresses in the ordinary type of spermatozoon by a gradual elongation, the nucleus forming the greater part of the head, and the protoplasm, the tail, as has been described in the NATURALIST for July, 1877 (p. 397). These changes are so striking that they have absorbed the attention of investigators; hence the relation of the spermatoblasts to the parent-cell has been far less studied than its importance demands. At present, certainly, it is impossible to give any general account of the development of the spermatozoa. I shall, therefore, confine myself to a *résumé* of Semper's observations of the process in the sharks, his being the most complete special account of which I know. The principal stages are represented in Fig. 8, which are taken from preparations stained with hæmatoxyline.

In the earliest stage the spermatoc follicle, or ampulla, *α*, is a cavity occupied by the remnants of a cell, which soon disappears. This cavity is lined by a layer of cells with large spherical, granular nuclei, and enclosed by an outer layer of cells with smaller dark, oval nuclei. The inner layer alone is directly concerned in the formation of the spermatozoa. In each one of the inner cells, which are the spermatocysts, the nucleus begins to multiply, as shown in *b*, *c*, *d*, *e*, dividing every time into two parts, one of which remains at the inner extremity of the cell and preserves the character of the parent nucleus, while the other recedes towards the outer end. The parent nucleus then again divides, until finally the spermatocyst contains one mother nucleus (*mutterkern*), and several daughter nuclei, which are easily distinguished by their

¹ The term spermatocyst has been used in various senses, but I believe the definition above given accords with the usage most widely accepted.

spherical shape and finely granular appearance. The daughter nuclei multiply by division. While these changes occur, the whole cell or spermatocyst becomes greatly elongated. At the completion of this stage, the parent nucleus at the inner end of the cell disappears, and a nucleus similar in appearance appears at the outer end, *f*. It is probable, but not demonstrated, that the two nuclei are identical, in other words, that the parent nucleus

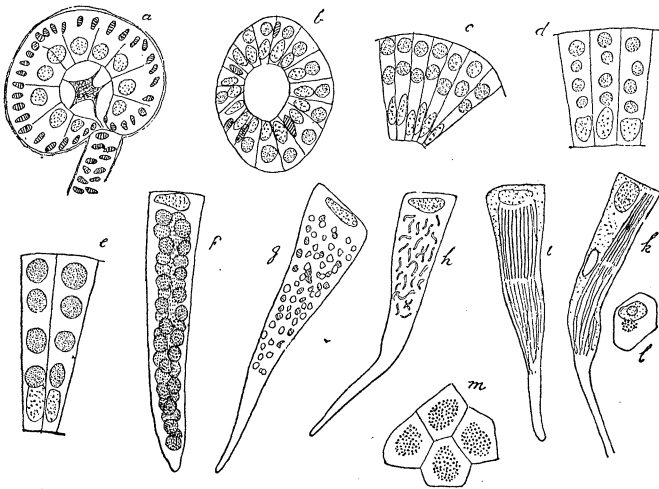


FIG. 8.—Development of the spermatozoa in sharks, after Semper.

migrates from one end to the other. The upper nucleus henceforth is passive, remaining behind to degenerate after the spermatozoa have been discharged from the cyst. Each one of the daughter nuclei, after subdividing still further so as to become very small, *g*, gathers a distinct mass of protoplasm around itself, and becomes a *spermatoblast*. The further development proceeds by alteration of the shape of these bodies: the nucleus elongates, becomes S-shaped, *h*. The elongation advances, the nuclei become straight and rod-like, and lie parallel to one another in the upper end of the cell, *i*. If we look at the cells from the outer surface of the ampulla, the center of the end of each cell is occupied by a cluster of dots corresponding to the bundle of rod-like nuclei seen endwise, *m*. Each long nucleus forms a spermatozoon head, which is connected with a thread-like tail. The development is completed by the discharge of the bundle of spermatozoa, leaving the large nucleus behind.

The essential feature of this whole history is, that a cell with a

single nucleus divides to form a compound body in which there is one large element with one kind of nucleus and numerous small elements, all with nuclei similar among themselves, but different from the single larger nucleus. The same thing occurs when the egg *sensu stricto*, or the thelyblast, is developed. In the case of the egg, it is the larger element which is preserved as the *female* part; in the case of the spermatocyst, it is the smaller elements which are preserved as the male parts. The two processes are complementary.

These facts have led to the following hypothesis of the relation of cells to the sexual elements. In an ordinary cell the two elements are intimately united in a latent condition, so that an ordinary cell is hermaphrodite or neuter, sexless, by which I mean it has no sexual differentiation. Diagrammatically this condition may be represented by Fig. 9, *A*. To form an egg the male portion is removed in several parts, which are the polar globules, while one large portion becomes the egg or thelyblast, Fig. 9, *B*. To form the spermatozoa, the two elements separate, the mother nucleus, or female part, remains behind, and if my hypothesis is correct, it, as well as the egg, must be called a thelyblast; the spermatozoa are discharged, and are capable of further vitality. They are the homologues of the polar globules. For both structures the common name *arsenoblast* has been suggested. If the

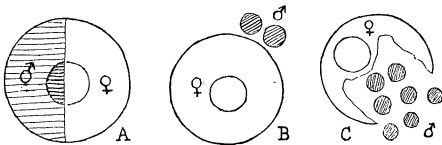


FIG. 9.—Diagrams to show the relation of the sexual products to cells. *A*, an ordinary cell; *B*, egg with polar globules; *C*, spermatocyst with spermatozoa.

above hypothesis is valid, then there is a fundamental distinction between cells on the one hand, and the *genoblasts* (the sexual products) on the other—every genoblast contains only one sexual element,

every cell contains both. When sexual reproduction occurs, a thelyblast from one source unites with an arsenoblast from another source—the two by their fusion complete a perfect cell, which is called the impregnated ovum. In the next article this process will be described.

In conclusion I wish to repeat that the conception of sex here advanced is only an hypothesis, which further research may cast aside, but which I hope may be confirmed, because it is already possible to bring forward many strong arguments in its favor.

For the convenience of those who may wish to pursue these subjects further, I quote below some of the principal articles, especially those which contain further bibliographical references :

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THE CONVOLUTION OF THE TRACHEA IN THE SANDHILL AND WHOOPING CRANES.

BY THOMAS S. ROBERTS.

IT is well known to ornithologists, that in many birds there are various peculiar modifications of the trachea, or windpipe, which, it is supposed, serve the purpose of adding some particular quality to the voice. Passing by the numerous minor instances of this structure as seen frequently in ducks, in some geese and a few other birds, we find it most strikingly exhibited among the cranes and swans. In certain species of these two groups the trachea enters the enlarged and excavated keel of the sternum, and after a number of convolutions, varying in position and extent with the species, passes out at the place of entrance and thence into the lungs. In such cases, at least, it is plainly great strength and volume of tone which are imparted, as is clearly evidenced by the powerful utterances for which these birds are noted.